Dynamics of Peripheral Populations of Great Basin Pocket Mice, *Perognathus parvus*, and Western Harvest Mice, *Reithrodontomys megalotis*, in Southern British Columbia

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The Great Basin Pocket Mouse (*Perognathus parvus*) and Western Harvest Mouse (*Reithrodontomys megalotis*) are two peripheral species occurring in the southern Okanagan Valley of British Columbia, Canada. Both species are listed as vulnerable to extirpation because of habitat loss, primarily due to conversion of natural habitat to agricultural uses and suburban expansion. Population dynamics of these two species were studied in three habitat types: old field, sagebrush, and pine forest. The Great Basin Pocket Mouse occurred at densities ranging from 12 to 28/ha in sagebrush habitats and at 2-8/ha in old fields and Ponderosa Pine forest. The Western Harvest Mouse occurred at variable densities up to 10/ha in old fields and up to 5/ha in sagebrush habitats. Mean number of lactating females for Great Basin Pocket Mice ranged from 4-8 in sagebrush, 1-5 in old fields and pine forests combined. Mean juvenile survival to adulthood ranged from 3.28 young Great Basin Pocket Mice per pregnant female in sagebrush, 4.67 in old field, and 1.82 in pine forest habitats. Mean juvenile survival to adulthood of Western Harvest Mice ranged from 1.46-1.72 young per female in old field and sagebrush habitats. Conservation of habitat features (high biomass and structural diversity of grasses and forbs) in linear habitats has the potential to maintain populations of Western Harvest Mice. The Great Basin Pocket Mouse needs features of sagebrush and old field habitats that need to be conserved as natural non-linear components in mosaics of natural and anthropogenic habitats. Both species could act as "indicators" of habitat integrity for a wide range of other vertebrate, invertebrate, and plant species in the Okanagan Valley.

Key Words: Great Basin Pocket Mouse, *Perognathus parvus*, Western Harvest Mouse, *Reithrodontomys megalotis*, old fields, population dynamics, reproduction, sagebrush habitat, conservation, dispersal, British Columbia.

A diverse group of terrestrial small mammals inhabits the intermontane grasslands and shrub-steppe rangelands of the Okanagan and Similkameen valleys of southern British Columbia, Canada. This ecological zone with its semi-arid habitats is unique within Canada and has many of the endangered species listed by the Species at Risk Act (SARA). According to Harper et al. (1993), there are species of vertebrates, invertebrates, and plants in the southern Okanagan that occur nowhere else in British Columbia, and some occur nowhere else in Canada. These authors reported that only 9% of the landscape was still in a relatively natural state to support this biodiversity because of habitat losses from agricultural (including cattle grazing), urban, and recreational developments.

There are two species within the small mammal community that are considered vulnerable: the Great Basin Pocket Mouse (*Perognathus parvus*); and the Western Harvest Mouse (*Reithrodontomys megalotis*). The subspecies *R. m. megalotis* is designated as of special concern by COSEWIC (2007*). On a provincial basis, the British Columbia Ministry of Environment has the Great Basin Pocket Mouse on the red list (endangered or threatened taxa) and the Western

Harvest Mouse on the blue list (species of special concern) (B.C. Conservation Data Centre 2007*). Both rodent species have peripheral ranges in the Okanagan and Similkameen valleys with much wider distributions in the United States. The Great Basin Pocket Mouse also occurs in the Kettle River and Thompson River valleys (Nagorsen 2005). A related subspecies of Western Harvest Mouse (*R. m. dychei*) has a very limited range in southern Alberta and is listed as endangered (COSEWIC 2007*).

The importance of these two species is linked to their status as indicators of the health and integrity of natural habitats and to the significance of peripheral populations for a species' ability to evolve new adaptations to changing environments (Hunter and Hutchinson 1994). As discussed by Lesica and Allendorf (1995), conservation of peripheral populations is likely beneficial to maintenance of the evolutionary process, but also protection of those environmental systems may generate future evolutionary diversity. Alternatively, Hoffman and Blows (1994) suggest peripheral populations may be prone to extirpation or hold little evolutionary potential due to low genetic variability.

The Great Basin Pocket Mouse is a semi-fossorial granivore that inhabits shrub-steppe habitats in the intermontane zone of western North America, in particular dry grassland and shrub associations on light-textured soils (O'Farrell et al. 1975; Verts and Kirkland 1988). Populations of Great Basin Pocket Mice in the United States seemed to have relatively stable populations from year to year with occasional high numbers in years of enhanced plant productivity (O'Farrell et al. 1975; Verts and Kirkland 1988). In British Columbia, Great Basin Pocket Mice are often sympatric with Western Harvest Mice: grassland-steppe composed of Big Sagebrush (*Artemisia tridentata*), Antelope-brush (*Purshia tridentata*), Bluebunch Wheatgrass (*Agropyron spicatum*), Prairie Sagewort (*Artemisia norvegica*), and Common Rabbitbrush (*Chrysothamnus nauseosus*) (Nagorsen 2005). Old fields and Ponderosa Pine (*Pinus ponderosa*) forest may also be used by Great Basin Pocket Mice (Nagorsen 2005). This species hibernates from mid-October to late March in the southern Okanagan Valley (Iverson 1967).

The Western Harvest Mouse inhabits various grasslands, edges (linear habitats), riparian habitats, and coastal salt marshes in western North America (Webster and Jones 1982). This rodent prefers habitats with abundant grass-dominated herbaceous vegetation (Kaufman and Fleharty 1974; Moulton et al. 1981; Kaufman et al. 1988). Populations of Western Harvest Mice in the United States exhibited a range of patterns of abundance from annual cycles (Brady and Slade 2004) to highly variable numbers (Skupski 1995) with a potentially strong negative interaction with vole (*Microtus* spp.) population peaks (Heske et al. 1984). In British Columbia, Western Harvest Mice may occur in shrub-steppe grasslands with abundant tall grasses such as Bluebunch Wheatgrass and shrubs such as Big Sagebrush and Antelope-brush (Nagorsen 1995[*], 2005) and in old fields (Sullivan and Sullivan 2004). This species is active year-round.

The native habitat requirements of these two species seem to be reasonably well documented, as well as data on population patterns in southern parts of their respective ranges in the U.S. However, there is a dearth of information on the population dynamics and status of either species in British Columbia and how such data might relate to conservation of native habitats and biodiversity. In particular, relatively long-term (i.e., 3-5 years) population studies provide insights into species persistence and help identify those habitats (both natural and managed) that should be conserved. Although abundance is important, the demographic attributes of reproductive performance, recruitment, and survival may be more important than numbers to determine habitat quality for small mammals (Van Horne 1983). Thus, this study was designed to compare the population dynamics of Great Basin Pocket Mice and Western Harvest Mice in a variety of habitats in the southern Okanagan Valley of British Columbia.

Materials and Methods

Study area

This study was located in the Okanagan Valley at the Pacific Agri-Food Research Centre, Summerland, British Columbia, Canada (49°34'N; 119°40'W). Three habitat types were examined: old field, sagebrush, and Ponderosa Pine forest, at an elevation range of 400-464 m and reasonably similar soil profiles. The old field sites were abandoned (≥ 25 years) hay fields dominated by Crested Wheatgrass (*Agropyron cristatum*) and Quack Grass (*A. repens*), with some Alfalfa (*Medicago sylvatica*) and herbs such as Yellow Salsify (*Tragopogon dubuis*), Great Mullein (*Verbascum thapsus*), American Vetch (*Vicia americana*), Prickly Lettuce (*Lactuca serriola*), and Tall Tumble-mustard (*Sisymbrium altissimum*) (Figure 1). These sites were each 2-3 ha in area. The sagebrush sites were natural habitats that have been relatively undisturbed, except for some grazing by feral horses. In addition to sagebrush and rabbit brush, these sites had Bluebunch Wheatgrass, Downy Brome (*Bromus tectorum*), Diffuse Knapweed (*Centaurea diffusa*), Yellow Salsify, and Six-weeks Fescue (*Vulpia octoflora*) (Figure 2). These sites were each 5-6 ha in area. The Ponderosa Pine forest sites were also natural habitats which have had little disturbance, except for grazing by horses. Ponderosa Pine was the major tree species with Bluebunch Wheatgrass, Downy Brome, Balsamroot (*Balsamorhiza sagittata*), and Diffuse Knapweed as the dominant herbs (Figure 3). These sites were each 5-6 ha in area. All study sites were located in the Bunchgrass and Ponderosa pine biogeoclimatic zones (Meidinger and Pojar 1991).

Experimental design

The study had a completely randomized design with three replicate sites of each habitat type. The 9 sites (3 habitat types × 3 replicates) were selected on the basis of availability of reasonably uniform vegetative characteristics of a given habitat type and proximity to one another. All sites were spatially segregated (0.20 – 0.62 km apart) to enhance statistical independence (Hurlbert 1984).

Population dynamics

Populations of Great Basin Pocket Mice and Western Harvest Mice were sampled at 4-week intervals from April to November 1999, April to October 2000, April to December 2001, and April to August 2002; and for logistical reasons of winter snow cover, at 5- to 8-week intervals from December 2001 to March 2002 and from August 2002 to March 2003. One trapping grid (1 ha), with 49 (7 × 7) trap stations at 14.3-m intervals, and one Longworth live-trap at each station were located in each site. Traps were supplied with whole oats and carrot, with cotton as bedding. Traps

FIGURE 1. Photograph of the old field habitat at Summerland in the Okanagan Valley, south-central British Columbia, Canada.

were set on the afternoon of day 1, checked on the morning and afternoon of day 2 and morning of day 3, and then locked open between trapping sessions.

All animals captured were ear-tagged with serially numbered tags, breeding condition noted, weighed on Pesola spring balances, and capture coordinates recorded. Breeding condition was noted by the size of testes in males and mammaries (lactation) in females (Krebs et al. 1969). Animals were released on the grids immediately after processing.

Other terrestrial small mammals that occurred in the study area included the Deer Mouse (*Peromyscus maniculatus*), Montane Vole (*Microtus montanus*), Long-tailed Vole (*Microtus longicaudus*), Yellow-pine Chipmunk (*Tamias amoenus*), House Mouse (*Mus musculus*), Wandering Shrew (*Sorex vagrans*), and Short-tailed Weasel (*Mustela erminea*). Seasons were defined as summer (April to September) and winter (October to March) periods. Thus, there were four summer and two winter periods that had at least five trapping sessions.

We used mass at sexual maturity to infer age classes of animals. Body mass was used as an index of age. The percentage of sexually mature animals was used to determine the mass limitations for juveniles and adults assuming that juveniles were seldom, if ever, sexually mature, and that at least 50% of the adults were sexually mature in their lowest mass class. Great

Basin Pocket Mice (juvenile = 1 – 18 g, adult ≥19 g) and Western Harvest Mice (juvenile = 1 – 10 g, adult ≥11 g) were classified as juvenile or adult by body mass. Recruits were defined as new animals that entered the population through reproduction and immigration. All handling of animals was in accordance with the principles of the Animal Care Committee, University of British Columbia.

Demographic variables

To compare the abundance of these two species in the different habitats, we measured trappability and population density. Jolly trappability was calculated according to the population estimates discussed by Krebs and Boonstra (1984). Population densities were estimated by the Jolly-Seber (J-S) model (Seber 1982) with small sample size corrections (Krebs 1991). Number of animals captured was used as the population estimate for the first and last sampling weeks when the J-S estimate was not calculated. The reliability of the J-S model declines when population sizes are very low and no marked animals are captured (Krebs et al. 1986). For these sample weeks, a minimum number of animals known to be alive (MNA) (Krebs 1966) value was used in place of a J-S estimate.

Measurements of recruitment, number of successful pregnancies, and early juvenile survival were derived

FIGURE 2. Photograph of the sagebrush habitat at Summerland in the Okanagan Valley, south-central British Columbia, Canada.

from the sample of animals captured in each trapping session and then summed for summer periods. Juvenile survival is an index relating recruitment of young into the trappable population to the number of lactating females (Krebs 1966). A modified version of this index is number of juvenile animals at week t divided by the number of lactating females caught in week $t - 4$. Mean survival rates (28-day) for summer and winter periods were estimated from the Jolly-Seber model.

Statistical analysis

A repeated-measures analysis of variance (RM) ANOVA (SPSS version 15.0; SPSS Institute Inc. 2007) was conducted to test for differences among habitats for the demographic variables of mean abundance, mean number of successful pregnancies, mean early juvenile survival, and mean J-S survival for populations of the two species. A univariate ANOVA was conducted on mean number of recruits for each species. A univariate ANOVA was also conducted within each period for significant site × time interactions in the RM-ANOVAs. Data not conforming to properties of normality and equal variance were subjected to various transformations to best approximate the assumptions required by an ANOVA (Zar 1999). Mauchly's W-test statistic was used to test for sphericity (inde-

pendence of data among repeated measures) (Littel 1989; Kuehl 1994). For datasets that were correlated among years, the Huynh-Feldt (H-F) correction (Huynh and Feldt 1976) was used to adjust the degrees of freedom of the within-subjects F-ratio. Duncan's multiple range test (DMRT) was used to compare mean values. We also calculated mean values for summer and winter periods, as well as for overall mean abundance with 95% confidence intervals (CI) for each species.

In all analyses, the level of significance was $P = 0.05$.

Results
Abundance

A total of 39 trapping periods were conducted from April 1999 to March 2003. The total numbers of individuals captured in the old field, sagebrush, and Ponderosa Pine habitats for Great Basin Pocket Mice were 139, 256, and 103 (total = 498), respectively, and for Western Harvest Mice were 189, 66, and 5 (total = 260), respectively. Estimates of Jolly trappability (susceptibility to capture) tended to be variable for each species, with overall mean values ranging from 50.2% to 61.8% for Great Basin Pocket Mice and 39.6% to 48.6% for Western Harvest Mice.

Population changes for Great Basin Pocket Mice indicated increasing numbers up to a peak density of

FIGURE 3. Photograph of the Ponderosa Pine forest habitat at Summerland in the Okanagan Valley, south-central British Columbia, Canada.

45.5 animals/ha in sagebrush habitats in 1999, with declining abundance in 2001 and 2002 (Figure 4A). Mean density of Great Basin Pocket Mice per ha was similar ($F_{2,6} = 3.48$, $P = 0.10$) among sites, ranging from lows of 12.0-13.7 to highs of 22.2-28.0 (Table 1). The very low numbers recorded in winter 2002-2003 likely reflect hibernation. Population changes of Great Basin Pocket Mice were very similar between the old field and pine forest habitats (Figure 4A). Highest mean overall density per ha consistently occurred in the sage habitat (19.0) compared with the old field (5.0) or pine forest (5.1) habitats (Figure 4B). This pattern occurred in all years except summer 2001 when the sage and pine forest had statistically similar numbers, based on the significant site × time interaction. The Great Basin Pocket Mouse was not captured during the winter seasons of sampling owing to hibernation.

Western Harvest Mice exhibited seasonal changes in abundance with significantly different mean densities among sites in winter ($F_{2,6} = 5.14$, $P = 0.05$), but not summer ($F_{2,6} = 4.27$, $P = 0.07$) (Table 1, Figure 5A). This mouse occurred primarily in the old field habitats, reaching annual peaks in abundance ranging from 5.3 to 10.5 animals per ha in the fall and early winter months (Figure 5A). This pattern was main-

tained in most seasons except summer 1999 and 2000 when the old field and sage sites had similar (DMRT, $P = 0.05$) densities (Table 1). Mean overall abundance of Western Harvest Mice per ha was highest in the old field (3.7) compared with the sage (0.8) and pine forest (0.05) habitats (Figure 5B).

Reproduction and recruitment

Reproductive performance was measured by the mean number of lactating females and was similar ($F_{2,5} = 3.07$, $P = 0.14$) among sites for Great Basin Pocket Mice (Table 2). The mean number of lactating females of Western Harvest Mice was also similar ($F_{1,4} = 2.32$, $P = 0.20$) among sites, but with 5.2 times, on average, as many females lactating in the old field as in sage habitats. This was a consistent pattern throughout the study. Another measure of reproductive effort was the percentage of adult males in breeding condition over the four summers. This metric was calculated over all captures, and hence provided a degree of difference among habitats for each species. Mean percentages, with sample sizes, of male Great Basin Pocket Mice breeding were 50.9 ($n = 55$), 61.2 ($n = 255$), and 42.9 ($n = 35$) in the old field, sage, and pine forest habitats, respectively. Mean percentages of adult male Western Harvest Mice breeding were 75.0
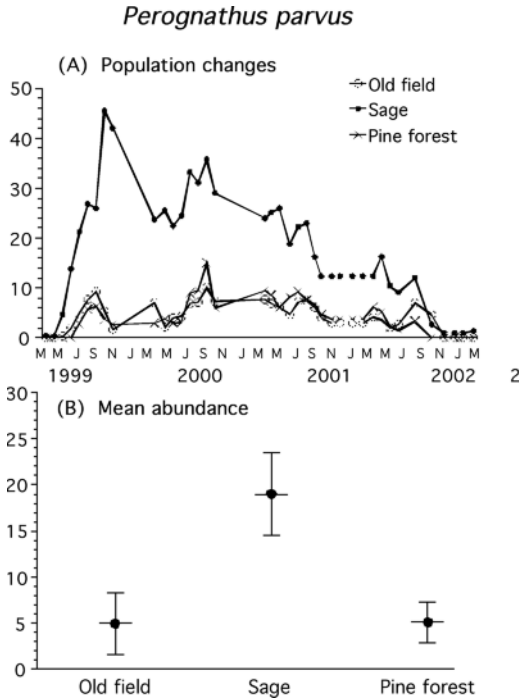
Perognathus parvus

FIGURE 4. (A) Population changes in mean number of animals per ha from 1999 to 2003, and (B) overall mean abundance per ha ± 95% confidence intervals ($n = 12$; 3 sites × 4 seasons) for Great Basin Pocket Mice in the three habitats at Summerland, British Columbia, Canada. M=March; M=May; J=July; S=September; N=November; J=January. Hibernation periods from mid-October to late March.
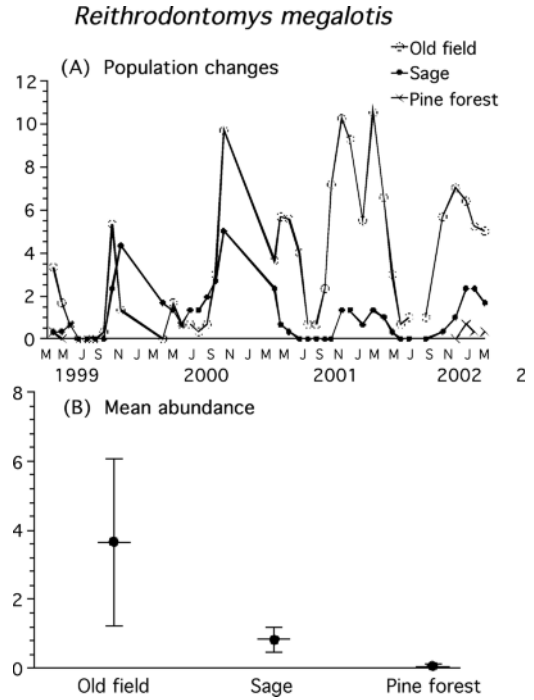
Reithrodontomys megalotis

FIGURE 5. (A) Population changes in mean number of animals per ha from 1999 to 2003, and (B) overall mean abundance per ha ± 95% confidence intervals ($n = 18$; 3 sites × 6 seasons) for Western Harvest Mice in the three habitats at Summerland, British Columbia, Canada. M=March; M=May; J=July; S=September; N=November; J=January.

($n = 52$) and 75.0 ($n = 16$) in the old field and sage habitats, respectively.

Recruitment of new Great Basin Pocket Mice and Western Harvest Mice was variable throughout the study and there were no statistically significant ($P > 0.05$) differences for any of the comparisons (Table 3). First captures of Western Harvest Mice were very few in the pine forest, but the 2.9-times higher number of total recruits in the old field (63.0) than sage (22.0) habitats was quite striking (Table 3).

Survival

The mean index of juvenile survival for Great Basin Pocket Mice was similar ($F_{2,5} = 2.49$, $P = 0.18$) among sites (Table 4). The mean total index was comparable in the old field (5.45) and pine forest (5.94), both 2.1-2.3 times higher than the sage habitat (Table 4). This measure of juvenile survival was quite variable for Western Harvest Mice, and hence there were no differences ($F_{1,4} = 0.44$, $P = 0.54$) between the two habitats (Table 4). Mean estimates of Jolly-Seber survival for male and female Great Basin Pocket Mice were

similar among sites during summer and winter periods (Table 5). Mean survival for Western Harvest Mice was variable, but was also similar among sites for both males and females (Table 6).

Discussion

Great Basin Pocket Mouse

This investigation follows that of Iverson (1967) in evaluating the population dynamics of the Great Basin Pocket Mouse in southern British Columbia, at the northern limit of its range. The Great Basin Pocket Mouse was 3.8 times more abundant in sagebrush habitat than in old field or Ponderosa Pine forest, indicating prime habitat for this heteromyid rodent. This finding was similar to reports for this species in other shrub-steppe habitats in western North America (O'Farrell et al. 1975; Verts and Kirkland 1988). Estimates of density per ha for populations of Great Basin Pocket Mice ranged from peaks of 42-82 in south-central Washington (Gray 1943; Hedlund and Rogers 1980). O'Farrell et al. (1975) reported sustained abun-

TABLE 1. Mean ± SE ($n = 3$ replicate sites) abundance per ha of Great Basin Pocket Mice and Western Harvest Mice during four summer and four winter periods within three different habitats and results of RM-ANOVA. F-values identified by * were calculated using the H-F correction factor, which decreased the stated degrees of freedom due to correlation of data among repeated measures (time periods). Mean values with different letters are significantly different by Duncan's multiple range test (adjusted for multiple contrasts). Within a row, different uppercase letters represent significant site differences as indicated by overall RM-ANOVA. Lowercase letters are used to indicate the location of significant differences resulting from univariate ANOVAs.

	Site			Overall RM-ANOVA					
				Site		Time		Site × time	
Species and period	Old field	Sage	Pine forest						
Pocket Mice									
Summer				$F_{2,6}$	P	$F_{3,18}$	P	$F_{6,18}$	P
Averaged over 4 summers	4.97±1.53	18.98±2.05	5.09±1.01	3.48	0.10	9.01	**<0.01**	0.56	0.76
1999	3.43±2.50	13.72±0.84	2.10±0.13						
2000	5.94±3.05	28.01±0.85	6.61±2.34						
2001	6.59±4.39	22.17±2.05	7.95±1.95						
2002	3.90±3.60	12.03±1.73	3.68±1.59						
Harvest Mice									
Summer				$F_{2,6}$	P	$F_{3,18}$	P	$F_{6,18}$	P
Averaged over 4 summers	1.88±0.54	0.62±0.20	0.01±0.01	4.27	0.07	4.89*	**0.02**	10.44*	**<0.01**
1999	0.86±0.79	0.19±0.19	0.05±0.05						
2000	1.00±1.00	1.56±0.42	0.00±0.00						
2001	3.22[a]±1.54	0.48[b]±0.27	0.00[b]±0.00						
2002	2.45[a]±0.68	0.27[b]±0.18	0.00[b]±0.00						
Winter				$F_{2,6}$	P	$F_{3,18}$	P	$F_{6,18}$	P
Averaged over 4 winters	6.85[A]±2.32	2.70[AB]±0.78	0.07[B]±0.04	5.14	**0.05**	1.21*	0.33	2.07*	0.11
1999/2000	3.33±2.62	3.33±1.88	0.00±0.00						
2000/2001	9.67±7.67	5.00±2.08	0.00±0.00						
2001/2002	8.53±5.11	0.93±0.13	0.00±0.00						
2002/2003	5.86±3.81	1.53±0.59	0.27±0.07						

TABLE 2. Mean ± SE ($n = 3$ replicate sites) number of lactating females for Great Basin Pocket Mice and Western Harvest Mice within three different habitats during four summer periods and results of RM-ANOVA. Mean values with different letters are significantly different by Duncan's multiple range test (adjusted for multiple contrasts). Within a row, different uppercase letters represent significant site differences as indicated by overall RM-ANOVA. Lowercase letters are used to indicate the location of significant differences resulting from univariate ANOVAs.

	Site			Overall RM-ANOVA					
				Site		Time		Site × time	
Species and period	Old field[1]	Sage	Pine forest						
Pocket Mice									
Summer				$F_{2,5}$	P	$F_{3,15}$	P	$F_{6,15}$	P
Averaged over 4 summers	1.88±0.48	5.92±0.87	1.92±0.74	3.07	0.14	2.02	0.15	3.84	**0.02**
1999	2.50[ab]±1.50	8.33[a]±0.33	0.67[b]±0.67						
2000	1.50[ab]±0.50	7.33[a]±2.19	1.00[b]±0.58						
2001	2.00±1.00	4.00±1.00	4.67±2.33						
2002	1.50±1.50	4.00±1.73	1.33±0.88						
Harvest Mice									
Summer				$F_{1,4}$	P	$F_{3,12}$	P	$F_{3,12}$	P
Averaged over 4 summers	2.58±0.93	0.50±0.19	/	2.32	0.20	6.94	**<0.01**	3.08	0.07
1999	0.00±0.00	0.00±0.00	/						
2000	1.33±1.33	0.67±0.33	/						
2001	5.00±2.65	0.67±0.67	/						
2002	4.00±1.53	0.67±0.33	/						

[1] $n = 2$ for Great Basin Pocket Mice in old field sites.

TABLE 3. Mean ± SE ($n = 3$ replicate sites) number of first captures for male and female Great Basin Pocket Mice and Western Harvest Mice during the four-year study and results of a univariate ANOVA.

Species	Old field[1]	Sage	Pine forest	ANOVA	
		Site			
Great Basin Pocket Mice				$F_{2,5}$	P
Males	34.0±18.0	44.3±4.4	17.0±5.9	2.92	0.14
Females	35.5±26.5	41.7±8.0	17.3±2.7	1.29	0.35
Total	69.5±44.5	86.0±10.8	34.4±8.4	2.03	0.22
Western Harvest Mice				$F_{2,6}$	P
Males	31.7±15.9	14.7±4.1	0.3±0.3	2.73	0.14
Females	31.3±19.1	7.3±1.9	1.3±0.9	2.05	0.21
Total	63.0±35.0	22.0±5.8	1.7±0.7	2.32	0.18

[1] $n = 2$ for Great Basin Pocket Mice in old field sites.

TABLE 4. Mean ± SE ($n = 3$ replicate sites) juvenile survival for Great Basin Pocket Mice and Western Harvest Mice within three different habitats during four summer periods and results of RM-ANOVA. F-values identified by * were calculated using the H-F correction factor, which decreased the stated degrees of freedom due to correlation of data among repeated measures (time periods).

Species and period	Old field[1]	Sage	Pine forest	Site		Time		Site × time	
		Site				Overall RM-ANOVA			
Great Basin Pocket Mice									
				$F_{2,5}$	P	$F_{3,15}$	P	$F_{6,15}$	P
Average of 4 summers	4.67±0.99	3.28±0.65	1.82±0.57	2.49	0.18	1.24	0.33	0.78	0.60
1999	5.50±0.50	2.48±0.05	0.83±0.83						
2000	7.50±0.50	4.06±2.32	3.50±1.89						
2001	3.34±2.34	2.83±0.34	1.84±0.64						
2002	2.34±2.34	3.75±1.75	1.11±0.59						
Western Harvest Mice									
				$F_{1,4}$	P	$F_{3,12}$	P	$F_{3,12}$	P
Average of 4 summers	1.72±0.77	1.46±0.94	/	0.44	0.54	2.83*	0.09	1.32*	0.31
1999	0.00±0.00	0.00±0.00	/						
2000	2.08±2.08	4.67±3.28	/						
2001	3.87±2.07	1.17±1.17	/						
2002	0.93±0.58	0.00±0.00	/						

[1] $n = 2$ for Great Basin Pocket Mice in old field sites.

dance of ≥ 80 pocket mice per ha in years of above average precipitation and subsequent high plant productivity. Studies seemed to confirm the positive relationship between autumn precipitation and seed resources (O'Farrell et al. 1975; Dunigan et al. 1980; Hedlund and Rickard 1981). Our populations of Great Basin Pocket Mice reached an average annual high abundance of 45/ha in October 1999 before declining over the next three years. Peak density per ha on one replicate site reached a high of 78 pocket mice during fall 1999, which was within the range of other published accounts. Declining abundance of this species may have been related to lower plant productivity, but we do not have records of relative growth of vegetation or precipitation for the four years of our study.

The sagebrush sites had the highest species richness of herbs and total species diversity of vascular plants (herbs, shrubs, and trees) of the three habitats (Sullivan and Sullivan 2006). Structural diversity (number of layers of vegetation and relative abundance in each layer) of shrubs was comparable in the sage and pine forest habitats with a negligible shrub layer in the old field habitat (Sullivan and Sullivan 2006). Thus, the cover provided by sagebrush and the richness and diversity of seed-bearing plants likely contributed to the preference for sage habitats by Great Basin Pocket Mice. Shrub cover has been reported to be particularly important for Great Basin Pocket Mice (Feldhamer 1979; Gano and Rickard 1982).

It may be biologically relevant that the sage habitat had consistently higher total and overall mean numbers (3.1 times) of lactating females than either of the old field or pine forest habitats. This pattern was recorded in all years except 2001 and 2002 where this measure of reproductive effort was similar among sites. Thus, the apparent higher productivity of Great Basin Pocket Mice in the sage habitat than other habitats tended to follow the pattern of greater abundance

TABLE 5. Mean ± SE ($n = 3$ replicate sites) Jolly-Seber 28-day survival for male and female Great Basin Pocket Mice within three different habitats during four summer and four winter periods and results of RM-ANOVA. F-values identified by * were calculated using the H-F correction factor, which decreased the stated degrees of freedom due to correlation of data among repeated measures (time periods).

Period	Site			Overall RM-ANOVA					
	Old field[1]	Sage	Pine forest	Site		Time		Site × time	
Males									
Summer				$F_{2,5}$	P	$F_{3,15}$	P	$F_{6,15}$	P
Average of 4 summers	0.71±0.06	0.82±0.04	0.80±0.05	0.47	0.65	0.34*	0.78	1.14*	0.39
1999	0.68±0.16	0.88±0.02	0.86±0.08						
2000	0.68±0.17	0.88±0.01	0.80±0.18						
2001	0.70±0.17	0.87±0.04	0.76±0.11						
2002	0.79±0.04	0.63±0.07	0.79±0.11						
Winter				$F_{2,5}$	P	$F_{3,15}$	P	$F_{6,15}$	P
Average of 4 winters	0.82±0.07	0.90±0.04	0.87±0.03	3.48	0.11	8.88*	**<0.01**	1.79*	0.18
1999/2000	0.85±0.03	0.99±0.00	0.86±0.05						
2000/2001	1.00±0.00	0.98±0.02	0.96±0.04						
2001/2002	0.81±0.08	0.95±0.01	0.83±0.03						
2002/2003	0.63±0.24	0.67±0.05	0.85±0.08						
Females									
Summer				$F_{2,5}$	P	$F_{3,15}$	P	$F_{6,15}$	P
Average of 4 summers	0.84±0.03	0.82±0.03	0.84±0.03	0.2	0.77	0.14	0.94	1.86	0.15
1999	0.84±0.07	0.87±0.06	0.74±0.06						
2000	0.82±0.04	0.86±0.03	0.87±0.09						
2001	0.74±0.03	0.82±0.04	0.92±0.06						
2002	0.95±0.05	0.73±0.10	0.82±0.02						
Winter				$F_{2,5}$	P	$F_{3,15}$	P	$F_{6,15}$	P
Average of 4 winters	0.81±0.07	0.85±0.05	0.85±0.03	0.12	0.89	28.68	**<0.01**	2.09	0.12
1999/2000	0.81±0.19	0.95±0.00	0.85±0.03						
2000/2001	0.95±0.05	0.95±0.01	0.94±0.01						
2001/2002	0.88±0.00	0.93±0.02	0.88±0.02						
2002/2003	0.59±0.20	0.55±0.04	0.73±0.04						
Total									
Summer				$F_{2,5}$	P	$F_{3,15}$	P	$F_{6,15}$	P
Average of 4 summers	0.75±0.03	0.81±0.04	0.79±0.04	0.31	0.75	0.91	0.46	1.30	0.32
1999	0.73±0.05	0.87±0.01	0.80±0.10						
2000	0.75±0.11	0.87±0.01	0.79±0.11						
2001	0.72±0.08	0.86±0.01	0.84±0.07						
2002	0.82±0.02	0.65±0.10	0.74±0.08						
Winter				$F_{2,5}$	P	$F_{3,15}$	P	$F_{6,15}$	P
Average of 4 winters	0.79±0.08	0.86±0.05	0.84±0.04	0.91	0.46	22.97	**<0.01**	1.31	0.31
1999/2000	0.88±0.13	0.98±0.01	0.85±0.06						
2000/2001	0.98±0.02	0.96±0.01	0.95±0.02						
2001/2002	0.81±0.11	0.93±0.02	0.89±0.05						
2002/2003	0.52±0.18	0.57±0.04	0.69±0.05						

[1]$n = 2$ for old field sites.

of animals in the sage sites. Females tended to have one or two litters (Verts and Kirkland 1988), but two pocket mice appeared to have three litters. One of these individuals lived in the sage and the other individual lived in the pine forest. Iverson (1967) also reported the occurrence of triple litters in Great Basin Pocket Mice. It may also be biologically meaningful that mean total first captures of Great Basin Pocket Mice were 1.2 times higher in the sage than in the old field habitats and this comparison was 2.5 times higher in the sage than in the pine forest habitats. In addi-

tion, total first captures of Great Basin Pocket Mice were 2.0 times higher in the old field than in the pine forest (Table 3).

Western Harvest Mouse

The Western Harvest Mouse is classified as a naturally rare species that occupies grassland and sagebrush habitats (Nagorsen 1995*). Our data support this observation documenting an overall mean abundance per ha 4.6 times higher in old field then sagebrush habitat. Although populations reached only 10 harvest mice per ha in the old field habitat of this study, a Western

TABLE 6. Mean ± SE (n = 3 replicate sites) Jolly-Seber 28-day survival for male and female Western Harvest Mice within three different habitats during four summer and four winter periods and results of RM-ANOVA. F-values identified by * were calculated using the H-F correction factor, which decreased the stated degrees of freedom due to correlation of data among repeated measures (time periods).

Period	Site			Overall RM-ANOVA					
	Old field	Sage	Pine forest	Site		Time		Site × time	
Male									
Summer				$F_{1,4}$	P	$F_{3,12}$	P	$F_{3,12}$	P
Average of 4 summers	0.78±0.05	0.86±0.04	/	0.62	0.48	4.19*	0.08	0.85*	0.44
1999	0.87±0.13	0.92±0.08	/						
2000	0.89±0.11	0.88±0.09	/						
2001	0.65±0.07	0.73±0.04	/						
2002	0.69±0.04	0.89±0.06	/						
Winter				$F_{1,4}$	P	$F_{3,12}$	P	$F_{3,12}$	P
Average of 4 winters	0.75±0.04	0.85±0.04	/	2.98	0.16	1.00*	0.42	2.76*	0.10
1999/2000	0.78±0.13	0.88±0.07	/						
2000/2001	0.81±0.04	0.70±0.06	/						
2001/2002	0.71±0.07	0.83±0.09	/						
2002/2003	0.68±0.07	0.97±0.03	/						
Female									
Summer				$F_{1,4}$	P	$F_{3,12}$	P	$F_{3,12}$	P
Average of 4 summers	0.77±0.06	0.93±0.03	/	2.65	0.18	3.85	**0.04**	2.92	0.08
1999	0.92±0.08	1.00±0.00	/						
2000	0.89±0.11	0.87±0.06	/						
2001	0.63±0.09	0.88±0.12	/						
2002	0.64±0.12	0.96±0.04	/						
Winter				$F_{1,4}$	P	$F_{3,12}$	P	$F_{3,12}$	P
Average of 4 winters	0.79±0.05	0.88±0.03	/	1.83	0.25	0.03*	0.99	1.61*	0.25
1999/2000	0.84±0.16	0.80±0.10	/						
2000/2001	0.83±0.04	0.85±0.08	/						
2001/2002	0.79±0.09	0.88±0.04	/						
2002/2003	0.69±0.06	0.97±0.03	/						
Total									
Summer				$F_{1,4}$	P	$F_{3,12}$	P	$F_{3,12}$	P
Average of 4 summers	0.71±0.07	0.82±0.05	/	0.81	0.42	4.07*	**0.04**	1.32*	0.32
1999	0.85±0.15	0.92±0.08	/						
2000	0.85±0.15	0.82±0.11	/						
2001	0.58±0.07	0.68±0.08	/						
2002	0.54±0.05	0.85±0.07	/						
Winter				$F_{1,4}$	P	$F_{3,12}$	P	$F_{3,12}$	P
Average of 4 winters	0.72±0.05	0.81±0.04	/	1.81	0.25	0.22*	0.86	1.81*	0.21
1999/2000	0.73±0.18	0.83±0.09	/						
2000/2001	0.80±0.02	0.68±0.06	/						
2001/2002	0.72±0.10	0.78±0.10	/						
2002/2003	0.62±0.08	0.95±0.03	/						

Harvest Mouse density peaked at 80 animals/ha in December in an irrigated old field with residual Alfalfa plants (Sullivan and Sullivan 2004). The mean (± SE) number of individuals per ha for that year were 29.2 ± 23.5 with other densities ≤ 10 animals/ha in less productive old field habitats (Sullivan and Sullivan 2004). Other habitats occupied by Western Harvest Mice in the Okanagan Valley included an unmanaged apple orchard where in one winter 10 harvest mice/ha were captured, and one animal/ha periodically occurring in managed apple orchards, hedgerows, and riparian habitats (Sullivan and Sullivan 2006).

The variable numbers of Western Harvest Mice, with peak density (up to 13/ha) in winter and very low densities in summer, were also reported by Skupski

(1995) in Arizona. Brady and Slade (2004) reported densities of Western Harvest Mice in old field habitat in Kansas ranging from 0 to about 27/ha. Similarly, in Kansas, Johnson and Gaines (1988) observed seasonal fluctuation in population densities, but with relatively constant numbers over several years. Blaustein (1981) reported that population densities of Western Harvest Mice fluctuated from 0 to 60/ha and 0 to 90/ha in disturbed grassland communities in California. Heske et al. (1984) also found periodic extirpations of harvest mice in California meadows with densities as high as 20/ha.

Our reproductive analysis of Western Harvest Mice supported the abundance pattern with more lactating females and recruits occurring in the old field than in

sagebrush habitats. Not surprisingly, the Western Harvest Mouse has been reported to have variable patterns of reproductive activity consistent with variable densities of mice through time in a given habitat (Brown and Zeng 1989; Skupski 1995). Lactating females were recorded in spring (March to May) and autumn (October-November) in the four years of this study.

The variable pattern of population dynamics of Western Harvest Mice in certain habitats may fit a source-sink dynamics pattern (Pulliam 1988; Skupski 1995). Thus, this rodent species may be able to persist among the "good" and "poor" habitats of a fragmented landscape. This potential is enhanced by its apparent dispersal ability (Whitaker and Mumford 1972; Ford 1977) and relatively high rates of recruitment in prime habitats (Sullivan and Sullivan 2004). Another possible explanation for the variable densities of Western Harvest Mice was competition with other small mammals, particularly *Microtus* spp. Abundance of Western Harvest Mice did seem less when there was high (>20/ha) numbers of montane voles in this study (Sullivan and Sullivan, unpublished) and in terms of interspecific competition (Heske et al. 1984; Johnson and Gaines 1988; Sullivan and Sullivan 2004).

Conclusions

Peripheral populations of Great Basin Pocket Mice and Western Harvest Mice in southern British Columbia had similar patterns of abundance to those reported in published accounts from other parts of their respective ranges. This conclusion suggested that the "abundant-center model" (Sagarin and Gaines 2002; Guo et al. 2005), whereby peripheral populations are less demographically viable than their counterparts closer to the geographic centre of their ranges, may not hold for these particular rodent species. Clearly, a concurrent evaluation of population dynamics of these species across their ranges would provide a rigorous test of this hypothesis.

The preference for sagebrush habitats by Great Basin Pocket Mice and its apparently poor dispersal ability, suggests that such sites, including old fields, need to be conserved as non-linear components within a mosaic of natural and anthropogenic habitats. Western Harvest Mice, on the other hand, may do well in linear and non-linear habitats with a high biomass and structural diversity of grasses and forbs. Various configurations of linear habitats in the form of hedgerows, field edges, fence lines, roadsides, and ditches may provide sufficient habitat for the Western Harvest Mouse if the vegetative component is maintained. To this end, linear habitats created within and bordering on the fields of agricultural crops (e.g., tree fruits and vineyards) could help curb the eroding habitat base for these species.

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